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MUTATIVE REVERSIONS IN COTTON.

BY

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MUTATIVE REVERSIONS IN COTTON.

INTRODUCTION.

It is customary for writers on heredity and breeding to look upon reversions and mutations as rare and exceptional phenomena, but mutative variations of the cotton plant are of frequent occurrence and many of them appear to be reversions. Knowledge of the nature, extent, and causes of such reversions would throw light upon many problems of breeding and adaptation of varieties, for variations of this kind appear to be one of the chief factors of deterioration.

Many pronounced variations occur in cotton as sequels of hybridization and among the diversities aroused by new conditions. Individual variations seldom appear to differ from the parent stock by a single feature, but usually show numerous peculiar characteristics outside of the ordinary range of variation of the parental types. The cotton plant affords an unusually favorable opportunity for the observation of such facts because so many of its parts are readily seen and compared.

Changes of characters are not confined to stocks that have been recently hybridized. Even in the most uniform varieties, such as the Triumph Upland cotton of Texas, many individual plants may show sudden departures from the normal characters of the variety, especially when the conditions are new or extreme. The nature of such variations and the frequency with which they occur indicate that they represent reversions to the earlier diversities of the type that have been suppressed by selection.[a]

Reversion may be defined as the return of ancestral characters to expression. Plants or animals that differ from their immediate relatives in showing characteristics of remote ancestors are described as reversions, or "throw-backs." Striped pigs, black lambs, blue pigeons, red ears of corn, and brown-linted cotton plants that appear occasionally in pure-bred white varieties may be looked upon as reversions to the characteristics of colored ancestors. Reversions may be reckoned as partial if the variant individuals bring into expression only a few of the ancestral peculiarities and in other respects continue to resemble the typical members of the breed.

[a] Local Adjustment of Cotton Varieties. Bulletin 159, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 20.

Reversions may be called total or complete when there are changes of whole series of characters of parent varieties.

REVERSIONS SIMILAR TO MUTATIONS.

Whether wild species originate by sudden mutative variations or not, there can be no doubt in the case of the cotton plant that definite variations occur and that they can give rise to new cultivated varieties. The great majority of such variations are not preserved because they are inferior to existing types. In a uniform, big-bolled type of cotton, such as the Triumph, many small-bolled individuals with different habits of growth and other peculiarities may suddenly appear.[a]

In dilute hybrid stocks of Egyptian cotton, with only a small proportion of Upland or Hindi blood, individual plants of apparently "pure" Upland or Hindi cotton are found, while the other plants of the same ancestry show only the usual Egyptian characters. If the Egyptian parentage of these variations were not known it would not be suspected from any of the characters that are brought into expression. If the experiments had been conducted on a smaller scale and only the Upland or the Egyptian type had been familiar, these changes of characters might have been looked upon as rare mutations into new species, like those that occur in the garden variety of the evening primrose studied by Professor De Vries in Holland.

It does not seem probable that the mutative changes of characters that often occur in cultivated stocks of cotton represent the attainment of new characters, for the characters that come into expression in this way are commonly found among the more primitive types of cotton. Even the characters that have received the largest amount of selective "improvement" from breeders, such as large bolls and long, strong lint, have been found to exist in equal or greater degree in related types of cotton that have been cultivated only in tropical America without any conscious methodical selection by the Indians.

The more degenerate variations of the Upland cotton, with very small bolls and very short lint, are inferior to any of the varieties cultivated in the United States, so that they can not be looked upon as results of crossing with other varieties, except as crossing may be supposed to induce reversions. It is not necessary to suppose that these inferior characters are new, for some of them are closely paralleled among the very diverse forms shown by the Kekchi and other primitive Upland types that have been introduced from tropical America and acclimatized in the United States in the last few years.

Several of these newly introduced varieties also share the same characters that render the Hindi variations of the Egyptian cotton so strikingly different from the typical Egyptian plants, such as the

[a] Local Adjustment of Cotton Varieties. Bulletin 159, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 17.

shorter lobes of the leaves, the paler green color, and the thinner texture. Two or three of the calyx lobes of the Hindi cotton are usually drawn out into a long, slender tooth, a peculiarity previously observed only among the Central American cottons. Mr. Rowland M. Meade has found that the lobes of the calyx of the Hindi cotton are sometimes three-toothed, as also occurs in the Rubelzul cotton, a perennial Upland type from eastern Guatemala with long, pointed, Egyptian-like bolls. The bolls of the Hindi cotton have a rounded conic form and are abruptly apiculate. The surface is smooth and even, with the oil glands deeply buried in the tissues, another tendency shared with several of the Central American Upland cottons.[a]

The agreement of the Hindi with the Central American types of cotton extends even to the frequent display of two types of foliage among unacclimatized plants. Both types yield occasionally large, luxuriant, sterile, or late-maturing plants with deeply channeled five-lobed and seven-lobed leaves. Smaller and more fertile plants have the leaves more nearly plane, with only the usual three lobes regularly developed. Very vigorous Hindi-like plants often have the same general appearance as Egyptian-Upland hybrids and may represent hybrids between the Egyptian cotton and the extreme form of the Hindi. The large size may be connected with the fact that characters of both of the parent types are brought into expression. No tendency to unusual luxuriance appears in Egyptian-Upland hybrids that show the characters of only one of the parent types. The unusual vigor appears to be a physiological phenomenon in some way connected with the tension or conflict in the expression of the divergent characters rather than a consequence of sterility. The abnormal vegetative vigor begins to be manifested in the earlier stages of growth, before any of the plants have reached bearing age.[b]

The close similarities of the variant forms of the many different kinds of cotton may be taken to indicate that ancestral characteristics are returning to expression. Otherwise it would need to be assumed that the many different kinds of cotton are engaged in the formation of closely parallel series of new species. Whether the cotton variations be looked upon as mutations or not, it is equally desirable to recognize their relation to reversions. It might be as proper to call them revertive mutations as mutative reversions, except that the idea of reversion is older and better established than that of new species or new characters originating by mutation.

The range of ancestral diversities that may be expected to reappear in reversions must be learned by the study of the wild relatives of

[a] Origin of the Hindi Cotton. Circular 42, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

[b] The Vegetative Vigor of Hybrids and Mutations. Proceedings, Biological Society of Washington, vol. 17, 1904, pp. 83–90.

our domesticated plants. It is a mistake to think of natural species as uniform groups of plants that show only one set of characters, like our carefully selected varieties. Very few of our cultivated plants have so many wild or unimproved relatives as does the cotton, to serve as a basis of judgment regarding ancestral diversities and reversions.

RELATION OF REVERSION TO COHERENCE OF CHARACTERS.

Complete reversions may be considered as related to a phenomenon already described as coherence of characters.[a] In cotton hybrids there is a general tendency for the characters derived from the same ancestor to come into expression in groups or combinations. It seldom or never happens that a single character of one ancestor comes into full expression in a hybrid; that is, without being accompanied by the expression of other characters of the same parent. Coherence of characters appears to have a physiological significance. Among the hybrid plants that are superior to the parent stocks in vigor, fertility, and quality of lint, characters of both of the parental types are brought into expression in coherent groups. Hybrids that bring the characters of only one parent to full expression are not superior, while those that show incongruous combinations of characters are notably deficient in fertility. A notable example of this relation appeared in a field of Jannovitch cotton raised from imported seed at Somerton, Ariz., in 1909. The plant had the habit of growth, leaves, and bracts of the Egyptian cotton, but changed suddenly to Hindi characters in the long-toothed calyx, white flowers, and broadly conic light-green bolls. At the same time it retained the Egyptian characters of short stamens and long exserted stigmas. Though having great vegetative vigor, this plant was quite sterile. The anthers contained pollen, but did not open to shed it. The stigmas were abundantly cross-pollinated by insects, but no ovules developed and not a single boll matured.[b]

VARIATIONS OF DIVERSITY IN THE SAME STOCKS.

The fact that plants with a preponderance of Egyptian ancestry, such as three-quarters or upward, may show little or no sign of Upland admixture accords with the general tendency toward coherence in

[a] Suppressed and Intensified Characters in Cotton Hybrids. Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 16.

[b] The empty carpels of this plant showed a further peculiarity not hitherto observed. The ridge that marks the middle of the wall of the carpel, the line of dehiscence of the ripe fruit, gave rise to a series of long slender hairs that projected into the cavity. Hairs of the same kind were found afterwards in normal plants and may be looked upon as an additional storm-proof character, since they undoubtedly help to hold the lint and seeds in place after the carpels have opened.

the expression of characters, but coherence alone would not explain the further fact that plants of preponderantly Egyptian ancestry may depart from the Egyptian characteristics and appear as completely un-Egyptian Upland or Hindi. In stocks where the crossing upon the Egyptian is limited to half-blood Uplands there is a general reduction of the expression of Upland characteristics as compared with the crosses of full-blood Upland upon the Egyptians, but such dilutions do not preclude reversions to complete Upland forms.

Upland or Hindi characters that remain completely latent or without expression in one generation may recover their potency and return to complete expression in some of the members of the next generation. One planting of hybrid seed may show a preponderant resemblance to one parent, another planting to the other parent. One planting of a stock of seed may show none of the Hindi or Upland reversions, while another planting of the same stock of seed or another part of the same field may show very pronounced examples. Three plantings of the Jannovitch variety of Egyptian cotton in 1909 showed Hindi individuals of extreme form, although a large planting of the same stock of seed in 1908 gave only a few aberrant individuals in which comparatively slight evidences of Hindi contamination were detected.[a]

A question may still be raised regarding the authenticity of this extreme example where complete reversions have seemed to take place, as it were, by wholesale. Although there is no reason to doubt the equality and general uniformity of the imported Egyptian seed, it is still possible to imagine that the seed planted in 1908 was of different origin from that grown in 1909, even though both came from the same imported stock. Such possibilities as the sinking of the smooth Hindi seeds to the bottom of the bag, or failure to germinate, or early death of the Hindi seedlings have also to be reckoned with, though the chances that such accidents could afford any complete explanation of the facts appear very remote. The consistent general behavior of the Egyptian plants in the different fields and experimental plats and the general scattering of the Hindi individuals in the plantings of 1909 give no support to the idea that the seed was different. An absolute determination of the matter will require the study of more numerous and still larger plantings of seed, mixed with special thoroughness to avoid the possibility of accidental segregation of any of the different qualities that may be included.

Regular field plantings of Egyptian cotton can be made to serve the purposes of such experiments, but it is desirable to present in advance the collateral evidence for expecting that reversions will occur and that they are likely to appear in different numbers and

[a] A Study of Diversity in Egyptian Cotton. Bulletin 156, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, pp. 18–21.

degrees in different plantings, even when the seed is of the same stock. Though breeding is undoubtedly a very important factor in reducing diversity, it is no less important to ascertain the relations of environment to the occurrence of reversions. Such differences of behavior are frequently shown by the reversions of the Upland cotton, and the irregular variations of the Egyptian cotton appear to be susceptible to such influences.

Other forms of reversions, both partial and complete, have shown relation to differences of environment in experiments with cotton. Ancestral characters that are prominent in one locality may be entirely suppressed in another place where some of the same lot of seed has been planted. Not only the amount or degree of reversion but also the frequency with which particular characters are brought into expression is subject to change through differences of external conditions. The failure of any complete Hindi reversions to appear in the Jannovitch planting of 1908 does not appear merely arbitrary or accidental from the point of view of other experiments, but may be connected with the facts that the seed was sown rather late and that the plants developed under conditions of abundant moisture and heat that have shown a very general tendency to bring the extreme Egyptian characters into expression. Grown under such conditions, plants that are known to be Upland hybrids usually take on the complete Egyptian form and show very few Upland characters—sometimes none at all.[a]

THE HINDI COTTON CONSIDERED AS A REVERSION.

Young plants of the Egyptian cotton share the foliage characters of the Hindi, including the reddening of the pulvinus, the wrinkled, swollen cushion where the veins meet, at the base of the leaf. If the Egyptian plants are kept small and stunted by unfavorable conditions the resemblance to the Hindi continues longer, so that plants that finally develop with typical Egyptian characters may be mistaken for Hindi. Late in the season there is another partial approximation of the foliage characters, for the Hindi plants generally lose the red color of the pulvinus that serves as one of the most conspicuous diagnostic features of the Hindi at early maturity and during the preceding stage of growth. The general colors of the leaves are also less distinctive in the latter part of the season, the Egyptian cotton often appearing somewhat lighter and some of the Hindi plants becoming darker.

Plants that do not show very distinct Hindi features in their habits of growth, leaves, bracts, flowers, or bolls may still betray Hindi

[a] Suppressed and Intensified Characters in Cotton Hybrids. Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, pp. 17–23.

tendencies in their naked seeds and short, sparse lint. In many such cases the petals are of a somewhat lighter yellow than usual, or the purple spot may not be so deeply colored, but paler petals and spots may occur without any other departure from Egyptian characters. No one character can be trusted as evidence of the presence of Hindi tendencies, nor is there any reason to suppose that a failure to show Hindi characters in one generation excludes their appearance in another, any more than with the small-bolled and other inferior reversions that appear in Upland varieties. Some of the Hindi characters, such as the naked black seed with short, sparse lint confined to one end, are a feature of many small-bolled reversions that appear in Upland cotton.

Instead of thinking of the Hindi cotton as a distinct independent type which has become hybridized recently with the Egyptian, it may be considered that the Hindi characters merely represent some of the extremes of variation of the Egyptian. Whether the two types were originally distinct or not may make little difference with the present facts. There seems to be no definite evidence of the independent existence of the Hindi cotton, either as an indigenous wild plant or as a domesticated variety. It would doubtless be easy to establish the Hindi cotton as a uniform "pure" stock in the same way that selection can establish uniform types from other variations of the Egyptian cotton, but it is a type that would hardly invite cultivation, even among savages. A pale-flowered tree cotton without a petal spot was described in Egypt by Vesling about 1640, and Fletcher is inclined to believe that this was the prototype of the Hindi cotton. The Egyptian cotton itself is supposed to have been brought from India to Egypt only about a century ago, but even on this reckoning the time has certainly been ample for the most complete intermixture to have taken place.[a]

The general absence of intermediate plants may be taken as an indication that recent interbreeding with Hindi has been avoided in the best of the imported Egyptian stocks, but at least a few individuals of the extreme Hindi type have been found in all. The remarkably close similarity of the extreme Hindi plants in all of the newly imported stocks also supports the idea that such plants represent complete reversions. It is very difficult to believe that all the stocks have had the same opportunities of securing recent intermixtures of pure Hindi seed. The more pronounced of the Hindi plants are as uniform among themselves as the Egyptian plants in the same stage of acclimatization. Indeed, they appear even more

[a] See Fletcher, F., "The Origin of the Egyptian Cotton," Cairo Scientific Journal, vol. 2, no. 26, November, 1908, p. 383.

uniform, perhaps as a result of the strong contrast between them and the normal Egyptian plants.

If the Hindi plants stood alone, they would be identified at once as members of a series of Mexican cottons related to our Upland type, but with definite differences. Some of the varieties contain many plants that combine the Egyptian with the Hindi characters, plants that may be viewed as ordinary hybrids, but the persistence and remarkable uniformity of the Hindi type can hardly be understood except by the analogy of complete reversions to the Upland type already known in experiments with Egyptian-Upland hybrids.

CONTRASTED CHARACTERS OF COTTON REVERSIONS.

Though complete reversion may not have been formally recognized as a phenomenon of heredity, it is believed that an examination of related facts will show a very general tendency of reversions to extreme expression of characters rather than to slight or intermediate expression. Even when only one character appears to be changed there is more likely to be a complete change than a partial one. Uniform, deep-red ears are a much more frequent reversion in corn than ears that are pale red or that have only a part of the kernels red. Black lambs are generally black all over, and only very rarely spotted, except upon the head. This remains true even when black males are regularly bred with white females, as on the elevated plateaus of Guatemala, where the Indians prefer the black wool. A few piebald sheep were finally seen in one flock, but only after many of the mixed flocks had been looked over in vain.

Similarly accentuated contrasts are found between the Egyptian cotton and the Hindi. The veins of the leaf of the Hindi cotton are united at the base into a larger and more prominent cushion, or pulvinus, than in the Egyptian cotton, and the pulvinus of the Hindi cotton is rendered the more conspicuous by its red color, which is shared by the upper side of the somewhat swollen end of the petiole, for about half an inch. In normal Egyptian cotton the pulvinus is pale green, like the other portions of the veins, or only slightly tinged with reddish, like the end of the petiole. Under some conditions the stalks and petioles of the Egyptian cotton take on a bright-red color like the pulvinus of the Hindi, but in spite of the reddening of most of the petiole the swollen terminal part and the pulvinus of the Egyptian leaf remain distinctly paler. Exactly those parts that are the most promptly and deeply reddened in the Hindi plants are persistently paler in the Egyptian.

The stalks and petioles of the Hindi plants may also redden with age, as in the Egyptian, and when this occurs the contrast of color is destroyed, for the red of the pulvinus and the swollen end of the

petiole fades out, so that these parts become paler than the remainder of the petiole, as in the red-stemmed condition of the Egyptian cotton. But even on the old Hindi plants the very young leaves whose petioles are pale have the pulvini red.

The contrast is not limited to the color alone, but is carried over into the hairy coverings of the same parts. The Hindi cotton, like the Kekchi and other Central American types of Upland cotton, has the pulvinus and the adjacent reddened part of the petiole naked or with only a few scattering hairs, even when the rest of the petiole is densely hairy. In the Egyptian cotton, on the contrary, the petiole is generally naked, except that hairs are to be found on the small pale area at the end where the Hindi cotton is naked and red. The pale-green pulvinus of the Egyptian cotton is also distinctly hairy, especially on young leaves.

A similar case of completely contrasted characters has been brought to my attention by Mr. G. N. Collins. Some of the Mexican varieties of corn have the leaf sheaths almost completely naked, while others have them almost completely clothed with a coat of fine hairs. The contrast is strangely accentuated by the fact that the sheaths that are otherwise naked have a narrow band of hairs along the margins, while the marginal band is naked in the types that have the hairy sheaths.

REVERSION IMPLIES CONTINUED TRANSMISSION.

The facts of complete reversion have a practical bearing upon problems of breeding and acclimatization. They warn us not to rely upon the hope of being able to effect a complete elimination of undesirable ancestral characters, in the sense of excluding transmission. There does not appear to be any direct relation between the visible expression of characters in a plant and their invisible transmission in the germ cells. Characters that remain latent in one generation may become patent in another. A stock that appears pure under one set of conditions may appear in another place to be seriously contaminated. The latent transmission of an undesirable character does no harm as long as the latent condition continues, but the return of such a character to expression may be a serious injury in a crop like the Egyptian cotton, where the uniformity of the fiber is a prime requisite.

Experiments with cotton do not indicate that tendencies to reversion are limited to particular descendants or to single characters acting independently, as sometimes inferred from the behavior of Mendelian hybrids. Though regular Mendelian relations are found in cotton, the phenomena of heredity are evidently not limited to the strictly Mendelian reactions between the characters. Students of Mendelism usually limit their studies to reactions between varieties

that have been brought into a condition of uniform expression of characters, but other kinds of reactions are not less interesting and important. The uniformity or "breeding true" of a few generations of individuals does not show that a stock is "pure" in the sense employed by many writers on Mendelism. The idea that the Mendelian relations of expression determine the "presence" or "absence" of the characters is a convenient assumption when the typical Mendelian behavior appears, but reversions to "latent" characters show that expression is no complete index of transmission.

The idea that the ancestry of our cultivated plants is to be traced back to uniform "pure" stocks that transmitted only single sets of characters finds no warrant in the study of the more primitive types and wild relatives of our domesticated species. Diversity of expression, instead of uniformity, is the rule in nature, and the transmission of the diverse characteristics does not cease when uniformity of expression is enforced through selection. Reversions show that the underlying inheritance of diversity is not completely lost, nor the power of the ancestral characters to reappear, even after long periods of suppression.

REVERSIONS INTERFERE WITH MENDELIAN EXPRESSION OF CHARACTERS.

The tendency to reversion has to be reckoned as a serious obstacle to the utilization of hybrid varieties unless the external conditions and the processes of reproduction are under much more complete control than with an open-fertilized field crop.

Mendel pointed out a very useful distinction in showing that two kinds of combinations of characters are represented among hybrids, some stable in expression and others unstable. Intermediate characters or reversions that arise from divergent tendencies of expression may occur with much regularity in the first generation of a cross, but may afterwards diminish or disappear. Even when the first generation shows uniformly intermediate characters, the later generations tend to revert to more complete expressions of the parental characters. The typical Mendelian relations appear in crosses between strains that differ by definite tendencies to bring certain characters to full expression or to leave them without expression, but it does not appear that the analogies of such characters are applicable to all kinds of plants or to all classes of hybrids.

Some writers on Mendelism have supposed that inheritance is governed by protoplasmic determinants, or "units," that are entirely separate and independent, so that some of them can be changed without disturbing the others, like changing the letters of a word or the words of a sentence. Individual words from related languages can

often be combined into a hybrid sentence without disturbing the general grammatical structure, much as "unit characters" appear to be substituted for each other in strictly Mendelian hybrids. In other cases the words of two languages do not prove to be direct equivalents, but require different grammatical relations. Sentences can no longer be translated piecemeal, by individual words, but have to be recast by whole phrases or clauses. Words derived from the same language tend to keep together in the hybrid sentence, in the same way that characters of diverse parental types hold together in expression. Hybrids that gave intermediate or combined expression of Egyptian and Upland characters in the early generations have shown a distinct tendency toward more exclusive expression of Upland characters in later generations, even when selected for the expression of Egyptian or intermediate characters.

If the existence of determinant particles or character units is to be assumed, it is more reasonable to suppose that the expression of the characters is governed by positional relations among the particles than by mere presence or absence of particles. The theory of positional relations of determinants was suggested by Mr. Walter T. Swingle, of this Department.[a] It has the advantage of accommodating a wider range of facts than the Mendelian theory. The establishment of definite positions among the particles would account for conditions of uniformity and for regular Mendelian ratios of expression, while mutative reversions and diversified hybrids can be ascribed to disturbances of the positional relations. Thus the positional theory admits the transmission of latent characters as a general condition of inheritance, whereas Mendelian writers have treated latency as an exceptional phenomenon requiring to be explained by additional theories.

Mendelian combinations of characters do not promise to attain great importance in cotton because of the general tendencies to reversions and correlations of characters that interfere with stable combinations between characters derived from different types. Reversions transgress the Mendelian program. They interfere with Mendelian dominance in the first generation and with Mendelian combinations and segregations of characters in the later generations. A Mendelian combination of the naked seeds of one variety with the abundant lint of another might be desirable, but naked-seeded hybrids are prone to revert to sparse lint, so that the yield is not likely to be maintained. Fuzzy-seeded types are preferred because of the greater abundance of lint.

[a] In a paper read at a meeting of the Society for Plant Morphology and Physiology, entitled "Some Theories of Heredity and of the Origin of Species Considered in Relation to the Phenomenon of Hybridization." Abstract published in the Botanical Gazette, vol. 25, no. 111, 1898.

REVERSIONS OF LATER GENERATIONS OF HYBRIDS.

Many attempts have been made to obtain early and prolific Egyptian or Sea Island varieties by crossing with Upland, and the first generations of such crosses often appear very promising. The difficulty is that the later generations not only revert to the parental types, but often go farther back, to the condition of remote unimproved ancestors. Instead of having longer lint than the Egyptian parent, as the first generation usually does, the later generations become inferior even to the Upland parent. Hybrids representing the fourth and fifth generations, grown at San Antonio, Tex., in the season of 1909, did not show a single plant with good Egyptian lint, and very few that were better than ordinary Upland. This extreme deterioration might be ascribed partly to adverse conditions, but first-generation hybrids grown under the same conditions produced excellent lint, longer and stronger than the Egyptian parent. These contrasts between the different generations show that the hybrids do not merely fail to fix particular combinations of the parental characters, but may first exceed the parents and then suffer serious deterioration. The characters of the lint that have received the most selection show the most striking deterioration. Such hybrids promise to have practical value only in the first generations. The problem of utilization turns upon the possibility of raising commercial quantities of hybrid seed.[a]

The fact that hybrids of later generations often show characters different from those of the first generation has been taken as proof of the Mendelian theory of separate transmission of contrasted characters. Characters that appear in all of the individuals of the first generation but not in all of the second or later generations have been ascribed to the presence of two independent Mendelian "factors" that are supposed to be transmitted separately, and not recombined in all the members of the later generations, but in only half of them.

This theory would explain why half of the second generation might fail to show a character that appeared in all of the first generation, but it gives us no suggestion of the complete disappearance of the long lint in the later generations of the cotton hybrids. There is no reason to suppose that the internal "factors" that produce the long lint in the first generation of a hybrid cease to be transmitted to the later generations, but there are serious differences in the external expression of the characters. Factors that influence the expression of characters have to be considered, not merely the possibilities of alternative transmission. A character that has been expressed in

[a] Suppressed and Intensified Characters in Cotton Hybrids. Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 15.

intensified form in the first generation may be reduced or suppressed in later generations.

It may be that more strictly Mendelian reactions might have been secured if the experiments had been preceded by courses of strict line breeding, as in many Mendelian investigations, but this would not insure results of practical value, because there is no way to enforce the Mendelian condition of self-fertilization in field cultures of cotton. It is also possible that a course of self-fertilization would have the effect of more definitely fixing the expression of the desirable characters, and render the later generations less liable to show variations and reversions. These questions are worthy of careful investigation, though such physiological effects of line breeding upon expression are not taken into account in the Mendelian doctrine of pure germ cells.

Uniformity is much greater and more easily maintained among the descendants of an individual mutation than in a hybrid stock. From the breeding standpoint this greater tendency to uniformity may be reckoned as the chief difference between the reversions that occur as mutations and those that are found among hybrids. The range of variation among the mutations appears to be as great as among the hybrids, and warrants the expectation that almost any desirable combination of characters may be found by persistent search.

The apparent tendency of mutative reversions to come true from seed suggests another possibility of making combinations of characters between diverse types whose hybrids fail to show definite Mendelian reactions. Instead of attempting to establish immediate unions between the characters of such species as the Egyptian and Upland cottons, attention may be given to the occasional mutative reversions that appear in dilute hybrid stocks. Such mutations might not have the special vigor and fertility of first-generation hybrids, but they might yield more uniform progeny. A stock of Egyptian cotton that had once been hybridized with Upland might furnish a series of mutative variations more promising for breeding purposes than a stock of diverse hybrids. The application of this method involves the difficulty of producing and giving careful study to the large number of reversions that might need to be inspected before a particular combination of characters could be found. Most of the reversions will be inferior, but an occasional superior type may be expected. Even among the Hindi-like variations of the Egyptian cotton there are some that are above the average of the Egyptian, in spite of the extreme inferiority of the lint characters of the extreme Hindi type.

AGRICULTURAL SIGNIFICANCE OF REVERSIONS.

If the Hindi characteristics continue to reassert themselves in the Egyptian cotton, complete reversion is a less serious obstacle to commercial uniformity than partial reversion. It is much easier to recognize and destroy the complete Hindi plants than the intermediate individuals that give only slight expressions of the Hindi characteristics.

In plantings of the superior Jannovitch and Nubari varieties the proportion of the complete Hindi reversions has exceeded that of the plants that show an intermediate or partial expression of the Hindi characters. This is in notable contrast with the behavior of a planting of the older and less improved Ashmuni variety, where a large proportion of the plants show some of the Hindi characters. Whether these differences should be ascribed to the more careful breeding of the Jannovitch and Nubari varieties or to the different conditions of the fields is not certain. It may be that the intermediate plants represent new or relatively recent crosses between the Hindi and Egyptian forms of plants, rather than partial reversions, but the large numbers of plants that show Hindi seed characters indicate a very general presence of Hindi tendencies, at least in the Ashmuni stock. In any case, the recognition of the complete reversions will assist the careful planter in learning to detect the Hindi characteristics, even in their less conspicuous degrees of expression.

Hybrids and extreme forms of reversions are not the only types of deterioration that must be guarded against if the need of a high degree of uniformity is to be met. Many plants that do not depart from the Egyptian characteristics will be found to fall far below the standards of an improved variety, either in fertility or in the qualities of the lint. There is no reason to suppose that uniformity can be maintained without continued selection in any field crop grown from seed.[a]

If reversions were to be looked upon as ordinary hybrids like those that result from recent crossing, it would appear impracticable to guard the crop from contamination, and hence impossible to obtain a uniform commercial product. No matter how carefully the fields of the Egyptian cotton may be isolated, variations may still occur that can easily be mistaken for hybrids. The difficulty of securing adequate isolation of the Egyptian cotton will be serious enough in any regions where Upland cotton is grown, but it need not be exaggerated by the condemnation of stocks that may continue to show reversions without recent contamination.

The occurrence of reversions in one locality or in one season need not stand in the way of early return to practical uniformity if an

[a] Local Adjustment of Cotton Varieties. Bulletin 159 Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, pp. 56–62.

adequate selection is maintained and favorable conditions are provided. Familiarity with the vegetative characters of the plants will enable the undesirable reversions to be rogued out before the time of flowering, so that crossing with such plants may be avoided. Tendencies to variation that are shown in the lint and the seeds can be rejected when the necessary selections are made in the fall to secure high-grade seed for the next season's planting. The influence of the external conditions upon reversions is only one of many indications that the uniformity of the crop, as well as the yield of fiber, will depend upon cultural methods as well as upon the seed that is planted.

CONCLUSIONS.

The phenomena of reversion in cotton are not confined to the changes of single characters, but may result in wide departures from parental types and bring different series of varietal characters into expression.

The return of ancestral characters to expression does not depend upon recent hybridization, but may be shown in abrupt, mutative variations of "pure-bred" stocks that have been selected for the uniform expression of a single set of characters.

Reversions may be aroused by new or unfavorable conditions of environment and may vary in extent and frequency with changes of external conditions. The uniformity of a stock in one place affords no assurance that diversity will not reappear in another locality. Diverse characteristics continue to be transmitted and may return to expression after many generations.

The variations of the different types of cotton have general similarities and may be arranged in parallel series. The general range of the ancestral diversities of cotton is also to be learned from the study of wild or unimproved types and from the diversities that interfere with the Mendelian expression of characters in hybrids.

The uniformity of the progeny of mutative variations renders them greatly superior to hybrids for breeding purposes. The possibility of obtaining superior mutative reversions from later generations of dilute hybrid stocks is worthy of investigation, especially in cases where desirable Mendelian combinations are not obtained in the earlier generations of hybrids.

The Hindi variations of the Egyptian are similar in their characters and behavior to some of the reversions that appear in Upland varieties and may prove to be forms of reversion rather than results of recent contamination with a distinct type of cotton.

The more pronounced forms of reversion in Upland cotton, like the Hindi variations of the Egyptian cotton, are readily distinguished by vegetative characters, so that they can be rogued out before the time

of flowering, to avoid the contamination of the stock by cross-pollination.

Partial expressions of Hindi and other inferior characters can often be detected in the lint and seed, even when not shown in the vegetative characters of the plants. Such tendencies are to be taken into account in the annual selection of seed.

It is also of practical importance to distinguish between the Hindi variations of the Egyptian cotton and the variations that result from crossing with Upland cotton. If reversions are mistaken for results of recent hybridization it may appear impossible to guard the Egyptian or other superior types of cotton from Upland contamination, though there is every reason to believe that distances of a few miles will afford complete isolation.

Approved:

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